XI. *Studies in* Rhynchophora. IV. *A preliminary note on the male genitalia.* By David Sharp, M.A., F.R.S.

[Read June 5th, 1918.]

Plate IX.

In its Transactions for 1912 the Entomological Society of London published a paper by F. Muir and myself on the male genital tube of *Coleoptera*. That memoir was intended to give an idea of the variety of structure of this part that exists in the Order. It should evidently be followed by a study of considerable extent of some one of the divisions of *Coleoptera*, so as to gain a knowledge of the constancy of the particular type of structure throughout that division.

In 1911 and 1912 Professor Nüsslin contributed to the Zeitschr. wiss. Insektenbiol. a paper entitled "Phylogenie und System der Borkenkäfer," in which he considers the male genital structures of the European *Scolytidae*. It is an excellent piece of work, but it is too limited to serve the purpose of instructing us as to the constancy of type of these structures in a large Family of the *Coleoptera*. The *Scolytidae* are a division of the *Rhynchophora*, and Nüsslin found the division to be highly polyphyletic; a view which I believe to be correct.

Some three years ago I commenced a study of the genital tube in *Rhynchophora*, but I have found it so long a task that I think it desirable to publish a preliminary note on the subject.

The *Rhynchophora* are probably the most extensive natural group of species existing in the animal kingdom. In the Munich Catalogue of *Coleoptera* 11.591 species of the group are listed. This was in 1871, and since then the number of described species has more than doubled. No general catalogue of the group of later date has yet appeared, but fragments have been dealt with in the Schenkling publication. One of these, the *Apioninae* (Col. Cat. Berlin, 1910), by H. Wagner, includes 1060 species, while the Munich Catalogue had less than 400. The other divisions of *Rhynchophora* show a similar increase, and yet there are large numbers of undescribed species in collections and fresh ones are constantly arriving, so that we may

conclude that 200,000 is a minimum number for the existing species, of which about 25,000 are described.

Hence it is not a matter of surprise that I have not yet been able to obtain a sufficient knowledge to enable me to speak positively as to the objects of my work. I am, in fact, unable to demonstrate the value of the male structures for taxonomic purpose, yet I have done enough to convince myself that they are probably of great value. But I fear the task I have undertaken is likely to prove too much for me to accomplish, and I therefore publish this preliminary note in the hope that it may help to remove certain misconceptions that are prevalent, and may be of use to other students.

The morphology of the male genital tube is really very simple. It may be reduced to an elongate continuous tube, which is made to appear shorter and more complicated by a system of invaginations, in some respects comparable to an old-fashioned telescope.

Certain of the parts have received names from previous writers, and, as I shall have to refer to these, I will here mention the more important, viz.:

1. Lindeman, Vergleichend-anatomische Untersuchung über das maenliche Begattungsglied der Borkenkaefer. Bull. Soc. Imp. Moscow, vol. 49, 1875, pp. 196–252, 5 pls.
2. Verhoeff, in Abdominal segmente und Copulationsorgane, etc. Deutsche ent. Zeitschr. 1893, p. 156, pl. iv, figs. 126–140.
3. Verhoeff, Ueber das Abdomen der Scolytiden. Arch. f. Naturgesch. 62, 1896, 1, pp. 110–141, 2 pls.
4. Hopkins, on the genus *Pissodes*. U.S. Dep. Agric. Ent. Techn. Ser. 20, part 1, 1911.
5. Nüsslin, as already referred to on the foregoing page.

Nos. 1, 3 and 5 refer to *Scolytidae*, a very exceptional and difficult group of *Rhynchophora*; while No. 2 is but brief, and comparative with other *Coleoptera*, and, again, No. 4 relates only to one genus. Hence the information as to the genitalia of the great division is very small.

In figs. 1 and 2 I give a scheme of the arrangement of the tube in *Rhynchophora*. These two figures are purely diagrammatic, and in some ways do not convey an accurate

idea: the membranous part that connects with the body is not exserted naturally; thus the symmetry is never so complete as they lead one to suppose, and it is also greatly interfered with by the muscles, as well as by constrictions, folds and pleats, and the alternations of very hard parts with delicate membranes. In some forms (such as *Cionus*) the tube can, however, be extended into a form comparatively more elongate than in fig. 2.

In these diagrams the hard (chitinised) parts are represented by thick lines, the thin lines being membrane. The features shown by these diagrams are constantly present in all *Rhynchophora*, except that the spiculum is absent in one division of the *Calandridae* and in *Platypidae*; and that in the group last named there are no true median struts, the basal prolongations of the median lobe being there projections with membrane between them.

The Abdomen.

The genitalia in *Coleoptera* are withdrawn into the abdomen and completely concealed. Although the abdomen is not morphologically a part of the genitalia, yet the two are so intimately connected functionally that neither can be comprehended fully without a knowledge of the other. There are, indeed, some who consider that the genitalia in whole or in great part are really modified parts of the abdomen, and Verhoeff entitles his paper on the genitalia of *Scolytidae*, a study of the comparative anatomy of the abdomen.

In *Rhynchophora* the abdomen is greatly modified at the base of the ventral aspect in coadaptation with the metasternum and hind coxae. On inspection five ventral plates are seen, and these in descriptions are called the first (basal) and so on to the fifth. There is membrane concealed at the point of junction with the sternum, and also a hard more or less perpendicular part or phragma. These parts (which are not visible except by taking off the abdomen) are considered to represent the sternites of two segments. This is rendered in the highest degree probable by the fact that the corresponding dorsal portion of the abdomen has seven plates in place of the five ventral ones.

In addition to the seven easily recognised segments there is an eighth one, the dorsal part of which is usually large, while its ventral plate is small; the ventral plate

is usually membranous in the middle so as to be two distinct plates, but sometimes it is entire, and this is a character of much taxonomic importance. This last ventral may be called the eighth, or the true last ventral, so that in the ordinary course of counting, we pass at once from five to eight. The two missing sternites are, as explained above, really to be found at the base. Lindeman did not recognise this, and started the idea that one of these apparently missing plates was to be found in the genital tube in the form of the spiculum gastrale. If that view be adopted, we have really nine abdominal sternites and only eight tergites.

One of the complications in counting the abdominal segments is found in the case of the family *Belidae*, where there are superficially visible only seven dorsal plates. This, however, is due not to any real deficiency, but arises from the eighth segment being of very peculiar form, and telescoped into the segment preceding it.

In the Australian *Belidae* the concealed terminal segment can be easily pushed out, and is then found to be of very extraordinary shape, the dorsal plate being bent so as to have as great a surface on the ventral aspect as on the dorsal, and thus there is the simulation of an additional sternite. In the North American *Ithycerus* (which is only a subfamily of *Belidae*) the terminal segment is constructed as in *Belus*, but is exposed and not telescoped into the preceding segment. In this case there were, therefore, considered to be six (instead of the usual five) externally visible ventral plates; the error was, however, corrected by Dr. G. H. Horn many years ago (*cf.* Leconte, "Rhynch. of North America," p. 121).

The last dorsal is not of so great taxonomical importance as the last ventral; but it is subject to considerable modifications, one of which deceived Kolbe into describing it as the aedeagus. This error has been pointed out and corrected by Verhoeff. It is one that may be easily made in that particular case (*Rhynchophorus*), and it has unfortunately been copied in Packard's text-book; but it may be mentioned as showing the necessity of examining the tip of the abdomen when we are studying the genitalia.

The Spiculum Gastrale.

Close together, at the tip of the abdomen, we find to investigate the ventral and dorsal plates of the last segment, the termination of the alimentary canal, the junction

of the genital tube with the body wall, and a peculiar structure the spiculum gastrale. All these have origin from a membranous area at the tip of the abdomen, and this small and irregularly shaped membrane must be treated as common to all the structures. On severing this membrane so as to free the genital tube from the other parts, we expose the tegminal layer of the genital tube (the Paramerenrohr of Nüsslin). As this is the commencement of the genital tube it is well to remark that the posterior part of the tube is functionally its anterior part, as shown in fig. 2. This complication as to the orientation renders it desirable to use the terms basal and apical instead of anterior and posterior: basal being nearer to the centre of the body than apical is.

The spiculum gastrale is at once seen; it is the "Stengel" of Lindeman, the "fork" according to Hopkins, the "spiculum" of Verhoeff and Nüsslin. It is present in the great majority of *Rhynchophora*, but is absent in some of the *Calandridae*, especially in those of very large size, and it is also wanting in *Platypidae*. It is a curved or sinuate rod, connected at the apical area, mentioned above, with the tube at or near the base of the latter when extended; it is of variable size according to the species, and extends basally, its sinuation adapting it to some extent to keep close to the tube, its musculature is great. At its apex it forms a sort of fork with widely separated, short prongs; but there are various forms in which this structure is peculiar (cf. *Naupactus* and to a less extent *Episomus*). This part is closely connected with the true last ventral plate, and this connection appears to be not always a simple one. This structure is much in need of investigation, especially as some anatomists consider the spiculum to be a modified ventral plate (the 9th). At the other (or basal) extremity the spiculum is generally somewhat expanded and more abruptly curved, and sometimes greatly so. The spiculum diverges from the tegminal layer, of which I consider it to be a part, just as the strut of the tegmen is a part of the tegmen.

The Tegminal Layer.

This part of the tube connects with the apex of the abdomen. It does not reverse or extend when the organ is functioning, but is held in place by its connections, including the spiculum and the true last ventral, so that

it forms a tube through which the median lobe protrudes. It includes basally the tegmen, but the apical part is entirely membranous and transparent, and is usually omitted in figures, though the tegmen itself is nearly always represented. In the paper by Muir and myself this membranous part is called the second connecting membrane, but we now consider it better to call this membranous area the first, and in the figures it is marked *im*1.

A very interesting feature is found in the Rhynchophorid group of the *Calandridae*, inasmuch as this membranous area is more or less strongly and completely chitinised, thus becoming to some extent similar to the "body" of the median lobe. In certain forms, referred at present to the group *Sphenophorides*, the spiculum proceeds from this chitinised part, and the structure then appears to resemble the tegmen. This condition is figured in the Transactions of the Society (1912, pl. 76, fig. 221*a*).* This condition is instructive, as it shows that a part of the tube that is usually membranous can become chitinised, and that chitinisation is secondary to the membranous condition; a fact that should not be lost sight of. The term "connecting membranes" is itself objectionable, as it tends to convey the idea that they are of secondary importance, and merely connect the hard parts, while the fact is the integrity of the tube is the primary object of the whole mechanism.

Proceeding basally along the tube we come to a chitinous structure of a more or less transverse nature, but differing greatly in the various forms of *Rhynchophora*; sometimes it forms a simple ring, at others an incomplete ring, but it is usually provided ventrally with a single strut projecting basad. This hard part of the circumference of the tegminal layer is the "tegmen" (Sharp and Muir), the "Gabel" of Lindeman, Verhoeff and Nüsslin. It is of great taxonomic importance, especially in the families of *Rhynchophora* that are separated from the *Curculionidae*; the part that is dorsal taking on there a great development (*Anthribidae*, *Brenthidae*, *Rhynchitidae*, *Microceridae*, *Brachyceridae*, *Belidae*, *Apionidae*, *Attelabidae*), all of which have a large "cap-piece," differing in form according to the family. In various forms of *Curculionidae* there is no cap-piece, this being, of course, the

* In the explanation of the plate this part is said to be the tegmen, which is an error; for "tegmen" read there "pseudo-tegmen."

case in the forms I have mentioned as having the tegmen in the shape of an incomplete ring.

Although I wish to avoid at present all points of ultra-morphology, yet I think it is only proper to remark that the functions of the tegmen as part of a mechanism are complex, and until they are ascertained—at any rate to a certain extent—we must merely make use of the fact of constancy or inconstancy, for taxonomical purposes. Verhoeff (Arch. f. Naturges. 62) treats the "Gabel" as "Paramerenreste."

So much doubt exists as to the ultra-morphology of "parameres" in *Coleoptera*, that the term has been altogether abandoned by Muir and myself. And this not because the term is a bad one, but because of the great amount of theory that is associated with it. As an instance of this I may mention that Verhoeff in the memoir cited states (p. 139) that "the parameres of male *Coleoptera* are the true genital appendages." From what follows it appears that he means by this that the median lobe is the equivalent of a body segment, or somite, and that parameres are the equivalents of appendages of a somite (*i. e.* of legs, or of palpi). Such a view is almost or quite metaphysical, and I hope that I may be doing an injustice to Verhoeff in believing that is what he is promulgating.

In *Rhynchophora* the structure of the tegmen and the condition of the membranous areas immediately adjoining it are complex and varied, so that a special memoir on this part will have to be prepared. I am not able to give any information of a thorough nature on the matter, and in some forms where the tegmen is complex (*Brachycerus*, *Microcerus*, *Anthribidae*, and others) I anticipate that a knowledge of the development will be essential, for there appear in some cases to be folds that have become solidified by chitinous exudation.

The tegmen is placed at a part of the tube where, according to observations of F. Muir, a primary invagination occurs in development. This of itself must give rise to folding or doubling of the walls of the tube at this spot, and this is probably the real starting-point of the tegminal complications.

The Median Lobe.

Near or at the tegmen there exists a turn down of the membrane, which results in the connection of the mem-

brane with the body of the median lobe; this intervening membrane has been called by Muir and myself first connecting membrane, but I here call it the second. This lies within the tegminal layer, and is, in fact, a continuation turning apicad thereof. It may be called the median lobe layer. This layer is mentioned by Nüsslin, who calls it "Penisrohr," but he does not mention that it is continuous with the other layer, being an invagination thereof, the tegmen being chitinised at or near the line of invagination. It must not be supposed that this point can be at once settled by a slight examination; for the doubling is usually complex, and accompanied by creases, as the folding of the dorsal part of the circumference may not be at the same transverse line as the ventral folding, and may be accompanied by a tuck or overlap. Moreover, this part of the tube is the subject of considerable variation in length according to whether the tegmen is drawn back or pushed forwards, or the median lobe extended; this membrane is often very crumpled up. Our fig. 2 shows it in an imaginary simple form, and it can in some forms, such as *Cionus*, be actually extended into something like that.*

This intervening membranous area—*im2*—is really common to the tegminal layer and to the median lobe layer; in repose it is crumpled up under the protection of the tegmen, but when the median lobe is extended as in fig. 4 the crumpling disappears.

The median lobe is called by Lindeman the "Körper," by Hopkins the "stem," by Verhoeff and Nüsslin the "penis." It differs so much in form that it is difficult to give a general description of it; for our present purpose we may merely say that in some forms (*Naupactus sulphurifer*, *Erythrapion*, etc.) it is a long slender hard tube, while in other cases it is more or less membranous along the dorsal surface except at the sides, and this form, which is very common, is shown in our fig. 3, and is well exhibited by Hopkins' plate xi of the "stems" of *Pissodes*, though his figures do not convey any indication of the fact that this trough-like structure is really a tube, the sides of the trough being connected by membrane.

Whatever the shape of the median lobe it always possesses in *Rhynchophora* basally a pair of projections which

* My daughter prepared for me a series of drawings to illustrate the elongation of the tube in *Cionus*; but as a whole plate would be required for it, publication must be deferred to a more favourable time.

we call the struts of the median lobe; Lindeman and Nüsslin call them "Füsschen," Verhoeff and Hopkins "femora": in Latin diagnostic I call them "temones."

These struts are present in all *Rhynchophora*;* and though wonderfully constant in the same species, they display much variety in the different forms. They are certainly of considerable taxonomic importance. Sometimes they are so short (*Lixidae*) that they escape notice if a short portion of *em* is left on the preparation. In other cases they are very long (in *Cycloterinus forcatus*, Kolbe, they extend far into the prothorax and are so slender that the aedeagus can only be extracted with great care). The form of the struts is also very constant in the same species. They are definitely elongations of the membrane, tubular, and filled with chitin; in certain cases this structure is evident; in some forms they appear to be disconnected from the body, but there is always a membranous connection, though the chitin may be deficient for a brief space. Such cases occur when the struts come off with a great elbow from the lobe (cf. *Sitones*). The struts are sometimes quite short, and assume the form of callipers; but so far as I know this is only the case in *Lixidae*.† The struts, besides being areas for muscular insertion, seem to be, to a certain extent, a protection to the invaginated sac when this extends basally beyond the body of the lobe. When the sac is elongate the struts are sure to be long. The composition of the body of the lobe shows important distinctions that are, I have no doubt, of taxonomic importance; see as to this *Calandridae*, *Brenthidae*, *Rhina*, etc.

The median lobe does not enter into the genital tube of the female, but only opens its terminal cloaca (not the internal cavity called by Stein the cloaca). On the dorsal surface of the median lobe, more or less close to the apex of the lobe (sometimes at the apex, as in fig. 3), there will be seen an area evidently different from the contiguous parts: this is the place where the evagination of the sac occurs, and has been called the median orifice, but is not an orifice, but only the spot where the sac is invaginated, or, as the case may be, inverted.

* They are not present in *Platypus*; the projections there found being of a different nature, as I have previously stated.

† In Hopkins' figures of *Pissodes* the struts are depicted as amalgamated at their termination: this is a mistake, nothing of the sort occurs in any *Rhynchophoron*.

The Sac.

The more intimate part of the copulatory mechanism is the sac (called by some "praeputial sac," though the name is a misnomer). This structure is predominately membranous though it has various chitinous bodies in its walls. This is the structure that enters the genital tube of the female, one of the functions of the median lobe being to bring this male structure into such a position that it can enter the female parts notwithstanding its membranous texture. It is protean in form, and exhibits the most wonderful diversities of shape. A comparatively simple form is shown in fig. 4, a more voluminous and complex one in figs. 7 and 8. In repose the sac is packed away inside the median lobe, but most frequently the apex of the sac projects more or less from the base of the median lobe, where it can be seen with the duct entering it. The sac has a variety of structures in addition to its marvellous development of lobes; these structures form the armature of spines and thorns, as well as of minute papillae, etc. In addition to this armature, there is an adjunct of the duct of an important nature, placed in the wall of the sac where the duct enters. In fact, this structure is the completion of the copulatory mechanism. The duct enters it, and when the sac is everted the apparatus is carried with it and becomes the apical part of the sac; the functional orifice is seated on this little mechanism, and it is at this spot that the sperm leaves the male part of the genital conduit and becomes the appurtenance of the female. I call this the transfer apparatus. It differs greatly in various *Rhynchophora*. Our fig. 5 shows it in *Polycleis plumbeus* (a South African Otiorrhynchid), and fig. 6 exhibits it more highly magnified. It is seen to consist of a median structure, into the base of which the duct enters, terminating at its apex; the frame part is subsidiary. A structure more or less like the median portion of the apparatus (fig. 6) is very common, and the form may be considered as a vase-like flagellum; sometimes by great elongation it becomes a slender or whip-like flagellum, which may be several times as long as the whole insect; but usually the flagellum is shorter than this. I have examined this structure in a series of species of the genus *Holonychus*, where it varies very greatly in development, being in some larger than the flagellum of *Polycleis* (fig. 6), while in other species it is minute and difficult to detect.

As the sac is the part of the coleopterous genital tube that has been hitherto least investigated, I shall venture to say a little more about it than my knowledge really justifies; for its study is much more difficult than that of any other part, so that it has been too often passed over entirely, or without a word as to its being the essential organ of intromission, to which the other parts of the mechanism are merely accessory. The membranous part of the sac—its walls and lobes and any chitinous armature borne thereon must be considered as conveyers of the transfer apparatus to the spot where it can be effective. The functional orifice appears to be always minute even when the other parts of the apparatus are voluminous. In the case of the very long whip-like flagellum it is most difficult to actually see the aperture, for the structure cannot be set on end, but the long and slender apparatus may be said to be as fine as it is possible for a chitinous duct to be. Now, though there can be no doubt that in many *Rhynchophora* the sac to be functional must be fully extended, for the sessile—or even very minute (in *Holonychus deflexus* and *H. gracilis*, spp. n.) transfer apparatus is situate at its extremity, we may nevertheless doubt whether in other cases anything more than a slight or partial eversion occurs. From this point of view the Otiorrhynchid forms assigned to the *Celeuthetides* are very interesting, for in some of them the length and tenuity of the sac render a total eversion of the structure very improbable. Fig. 9 (*Trigonops*, or *Heteroglymma*, sp. n.?, New Guinea) shows one of the longest and most slender of these sacs; it contains a rather long curvate flagellum, attached to the wall of the sac only at the base where it is a little swollen and notched. It will be noticed that there exists also in the interior of the body of the lobe another structure which has all the appearance of being a tube (fig. 9 *y*) through which the slender flagellum may be thrust and would then protrude sufficiently for intromission. All that appears necessary in this case is for the sac to be everted (or perhaps moved apically without eversion) so that the flagellum passes into the director and protrudes; possibly the director may then itself move apically to a greater or less extent.

The transfer apparatus of the sac reaches its greatest complexity in the *Scolytidae*. Hence it attracted the attention of Lindeman, who called the whole of the pieces

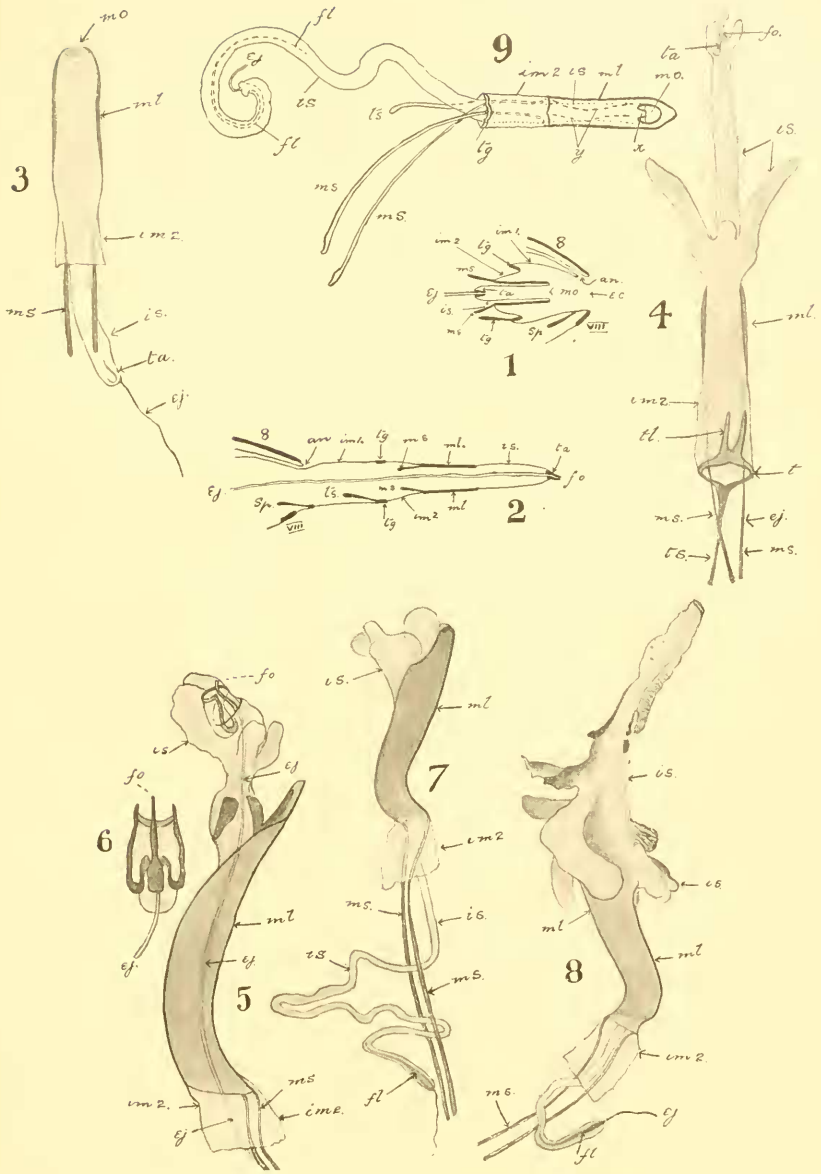
"Aufsatz," while Nüsslin prefers to call them the "accessory parts." Attempts have been made to homologise them, but sufficient is not known of their functions at present. The part on which the functional orifice is situate should be some guide, but this has hitherto been too much neglected. As to the other "accessory parts" little can be considered as settled. There are great differences in the inner structures of the tube in *Scolytidae*. The subject has been discussed at length by both Verhoeff and Nüsslin in their considerations of Lindeman's views. I can at present add nothing, though I may be permitted to say that it is not clear that the sac functions in all the groups in the same manner. As regards the variety in the "acessory parts" of the *Scolytidae* reference may be made to Lindeman's plates, and to Nüsslin's discussion of the point (Z. w. Insbiol., 1912, pp. 81–4). The necessity of caution in homologising from simple inspection is evident from the fact that Nüsslin considers the thirty-four genera of *Scolytidae* found in Germany to belong to at least twelve distinct subfamilies (*loc. cit.*, p. 206).

The Duct.

This is another part that needs special investigation, having been hitherto much neglected. It is sometimes extremely long. Of course if a very long sac has to be everted, there must be also a long duct, as this is carried as far as the sac is extended. Usually the duct is very easily seen, as it is surrounded by a very thick muscular coating, but this disappears on maceration and the canal is then fragile and difficult to detect. For the few particulars as to its course in *Scolytidae* refer to Nüsslin (*loc. cit.*, p. 20).

Methods.

The means of making a rapid examination of these parts are: have the insect to be dissected thoroughly penetrated by water, keeping it at or near the boiling point for a minute or two if small, for a quarter of an hour or more if large. Take off the abdomen and place it in a strong solution of caustic potash, having previously opened the abdomen at one side, so that the macerating fluid shall enter in readily everywhere. Leave it in the potash for a time varying, according to the size and delicacy of the specimen, from a few minutes to several hours. Take it out and put



MALE GENITALIA OF RHYNCHOPHORA.